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ORIGINAL ARTICLE

Natural treeless areas in the Krkonoše mountains: insights from two decades of pollen monitoring

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Abstract

Understanding past landscapes through sedimentary pollen records relies on precise knowledge of modern pollen–vegetation relationships. In mountain environments, however, altitudinal gradients, geomorphological complexity and prevailing air currents affect pollen deposition and make reconstructions of vegetation dynamics harder. This study investigates whether pollen assemblages can effectively differentiate between open habitats above and below the timberline (forest limit) in the Krkonoše mountains, or whether the effects of strong atmospheric circulation outweigh the diverging characteristics of these sites. We used 23 years of annual pollen trap data and vegetation surveys from 19 open sites distributed across an altitudinal gradient. Pollen deposition patterns were analysed using hierarchical clustering, ordination and dissimilarity analyses. Pollen assemblages from above and below the forest limit were statistically distinct, with differences driven mainly by quantitative variation rather than qualitative changes in composition of pollen types. The primary gradient was expressed by the proportion of long-distance transported pollen types, which dominated alpine and subalpine areas. Arboreal taxa formed a major component of background pollen, accompanied by low but consistent levels of wind pollinated herbs commonly interpreted as indicators of human impact. Other herbaceous taxa generally reflected their local presence, except for *Vaccinium*-t., which was under-represented. For sites above and below the upper forest limit, we characterised pollen composition in terms of percentages and accumulation rates, and established presence/absence thresholds for *Pinus*, *Picea*, *Fagus*, *Abies*, *Betula*, *Corylus*, *Alnus*, *Quercus*, Cerealia and *Urtica*. These findings improve our understanding of the role of long-distance pollen transport in high mountain treeless areas and provide baseline data for interpreting fossil pollen records from high elevation sites in Central Europe.

Keywords Annual pollen traps · Arctic-alpine tundra · Montane meadows · Pollen accumulation rate · Pollen–vegetation relationships

Introduction

Mountain regions present challenges for palaeoecologists aiming to reconstruct past vegetation from fossil pollen records. Steep altitudinal and geomorphological gradients, habitat diversity and strong air currents complicate the relationship between pollen assemblages and vegetation cover. A key focus in Holocene studies of mountain regions is the development of the upper forest limit, or alpine timberline, which separates forested or wooded areas from naturally treeless habitats. This boundary is typically gradual, as tree density decreases gradually, forming an ecotone zone around the uppermost patches of trees that define the treeline (trees are defined as being taller than 3 m; Körner 2012). The treeline ecotone is determined at its lower edge by the timberline and at its upper edge by the tree limit.

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Fossil pollen reconstructions alone, however, cannot usually resolve such fine distinctions and generally define natural treeless areas as lying above the timberline (Tinner et al. 1996; Hicks 2001; Tinner and Theurillat 2003; von Stedingk et al. 2008).

The formation of the treeline is primarily temperature dependent (Körner and Paulsen 2004; Paulsen and Körner 2014), with a global minimum daily mean temperature of 6.5 °C in the growing season (Paulsen and Körner 2014). This boundary has been highly sensitive to past climate fluctuations (Heiri et al. 2006; Büntgen et al. 2022) and is currently shifting due to ongoing climate change (Grace et al. 2002; Harsch et al. 2009; Wieser et al. 2014; Hansson et al. 2023). However, past human activities such as woodland clearance and grazing have strongly contributed to alter its position (Tinner and Theurillat 2003; Treml and Migoń 2015; Feurdean et al. 2016; Vincze et al. 2017). Understanding the dynamics of the treeline or forest limit is thus crucial for predicting the future of high altitude ecosystems and assessing long term ecological responses to environmental change.

The historical position of the forest limit can be reconstructed using pollen thresholds that define the presence of tree taxa. These are expressed either as pollen accumulation rates (PAR, grains cm^{-2} year^{-1}) or as percentages, with PAR preferred when chronological control is accurate (Seppä and Hicks 2006). Relative changes in its position can also be roughly estimated using AP/NAP (arboreal/non-arboreal pollen) ratios (e.g. Treml et al. 2008), though this approach is less reliable. The pollen thresholds at the treeline in boreal regions have been extensively studied in Fennoscandia, where trees reach their northern latitudinal distribution limit (Hicks and Hyvärinen 1999; Hicks 2001; Seppä and Hicks 2006; Jensen et al. 2007). Also, presence/absence thresholds for other contexts have been explored using a European network of annual pollen traps (Pidek et al. 2010, 2013; Lisitsyna et al. 2011; Abraham et al. 2021). However, local reference studies remain essential for refining pollen-based reconstructions, especially in mountainous areas, where specific relief, climate and vegetation composition significantly affect pollen dispersal and deposition.

High altitude regions receive pollen which has been transported vertically from lower down (Gaudreau et al. 1989; Markgraf 1980; Ortu et al. 2006). Combined with sparse local vegetation, this results in minimal local pollen input to high mountains and a strong influx of long-distance transported pollen (Markgraf 1980; Fall 1992; Abraham et al. 2017). This phenomenon is anticipated to be particularly pronounced above the forest limit in the Krkonoše, where anemo-orographic (AO) local wind systems are assumed to strongly influence pollen dispersal (Jeník 1961, 1997, 2008). Understanding how these wind systems affect pollen transport along elevation gradients is crucial for distinguishing local from regional pollen deposition, which in turn is necessary for accurate interpretation of pollen records and reconstruction of past vegetation and climate. When analysing sedimentary pollen records, it is important to consider both local and regional pollen sources to obtain a comprehensive view of landscape changes in time and space (van der Knaap 1990; Matthias and Giesecke 2014). Local pollen deposition refers to pollen grains originating from plants growing in the immediate vicinity of a sampling site, typically within tens of metres. Regional pollen deposition involves pollen grains transported over longer distances, often tens to hundreds of kilometres from their source, which may originate from various vegetation types that are absent locally (Janssen 1966).

In Europe, modern pollen–vegetation relationships, which are typically studied using moss polsters or modified Tauber pollen traps, have been investigated in the Alps, the Pyrenees and other mountain regions (for example, van der Knaap et al. 2001; Court-Picon et al. 2005, 2006; Fontana et al. 2023). These studies confirm that modern pollen samples generally reflect altitudinal zones. Whether this also holds for the specific environments of the Krkonoše mountains is examined in the present study.

The Krkonoše have some unique natural treeless habitats of arctic-alpine tundra above the alpine timberline formed by *Picea abies* (Norway spruce). This tundra, often referred to as a “tundra island” in Central Europe, has been shaped by both alpine and arctic influences and has several endangered glacial relict species (Jeník 1961; Soukupová et al. 1995; Kaplan 2017). Comprising both subalpine and alpine belts, it covers 47 km^2, making it the most extensive of its kind in these mountains (Treml 2004). The forest transition is gradual, forming a broad treeline ecotone often exceeding 100 m in width (Treml 2004). Here, trees suffer from an intensive summit syndrome, as the forest limit runs near the tops of ridges (Treml and Banaš 2000). Under such severe stress conditions, they regenerate mainly vegetatively and sexual propagation occurs only rarely in climatically favourable years (Šenfeldr and Maděra 2011). For pollen interpretations, their pollen production can therefore be largely neglected. As in the Fennoscandian region, trees in the Krkonoše reach the climatic limits of their distribution, but here this limit is expressed vertically along an altitudinal gradient rather than latitudinally. Given the shared geo-ecological features of arctic and alpine tundra habitats (Soukupová et al. 1995; Štursa et al. 2010), it remains unclear whether pollen–vegetation relationships in the Krkonoše follow similar patterns to those observed in boreal treeline regions or whether local environmental factors result in markedly different pollen thresholds.

In the Krkonoše, modern high altitude landscapes result not only from natural processes but also from historical human activities, which expanded treeless areas (Lokvenc 1995). Although numerous fossil pollen profiles have been analysed (Černohorské rašeliniště, Pančavská louka, Bílá louka, Úpské rašeliniště and Labský důl), modern reference studies linking pollen to local vegetation remain limited. Despite extensive research on pollen–vegetation relationships in various European mountain ranges, such studies remain scarce in the Krkonoše region. This gap makes accurate interpretation of fossil pollen records difficult, especially considering the influence of AO systems, past changes in treelines and difficulties with radiocarbon dating (Speranza et al. 2000, 2003; Jankovská 2001; Svobodová 2002, 2004; Treml et al. 2008; Engel et al. 2010).

Our study addresses this gap by investigating whether naturally treeless habitats in the Krkonoše can be identified by distinct pollen signals and distinguished from semi-natural montane meadows below the forest limit. We also aim to propose specific threshold values for presence/absence of key pollen types under modern conditions. We use long-term pollen monitoring data obtained from modified annual Tauber pollen traps, which have been in continuous operation since 1998 as part of the Pollen Monitoring Programme (PMP, Hicks et al. 1996, 1999). The traps are placed along an altitudinal transect ranging from 759 to 1,554 m a.s.l., covering a gradient from montane meadows surrounded by spruce-dominated forest to lichen tundra.

Research questions

(i) Is the position of the alpine timberline reflected in modern pollen assemblages? Can natural (primary) treeless areas be distinguished from semi-natural (secondary) treeless areas, or does the pollen from long-distance transport obscure this?

(ii) What is the primary factor influencing pollen distribution at our traps?

(iii) Do groups of pollen assemblages correspond to vegetation groups?

(iv) What are the pollen thresholds of key taxa indicating their presence or absence, in terms of absolute pollen accumulation rates (PAR) and relative percentages? Are these thresholds comparable to those in boreal treeline regions?

Addressing these questions will enhance our understanding of pollen transport mechanisms in complex mountain environments and improve the interpretation of past vegetation changes in the region.

Methods

Study area

The Krkonoše are the highest mountain range in Czechia with Sněžka (1,603 m) the summit, forming the northern fringe of Česká vysočina (the Bohemian Massif) along the Czech–Polish border. They cover 683 km^2, consisting of two main east–west oriented ridges connected by summit plains. On the Czech side, they form two parallel ridges separated by river valleys, while the Polish Silesian side features a steep tectonic slope. The climate is harsh, with cold winters, persistent fog and snow cover lasting approximately six months. The average annual temperature is ~0.2 °C and precipitation reaches ~1,200 mm. The main ridge is among the most wind-exposed in Europe, with frequent dry foehn winds in the northern part. Established in 1963, Krkonošský národní park, KRNAP (Krkonoše National Park), protects a unique mosaic of geomorphological features and natural environments shaped by specific geological characteristics and glacial processes, including glacial landscapes, natural treeless vegetation, and relict and endemic boreal-arctic species of plants and animals.

The annual pollen traps are distributed across three altitudinal zones, traditionally classified according to specific ecological characteristics and vegetation types:

The montane zone (800–1,200 m) is currently dominated by *Picea abies* (spruce) plantations, with some *Fagus sylvatica* (beech) and *Abies alba* (silver fir) forming mixed stands. Open areas of semi-natural grasslands are also present. Historically, traditional human-mediated management was widespread in the Krkonoše, primarily focused on the montane forest zone but extending into the subalpine zone. From the 17th century onwards in this region, the traditional land use in the montane and subalpine zones was for summer grazing of the mountain pastures and the herders stayed there in *boudy* (mountain huts) (Lokvenc 1960, 2007). The forest around these huts was transformed into secondary treeless vegetation with species-rich mountain meadows. Following the abandonment of traditional management, these meadows returned to forest again (Jiřiště 2000). Our study sites in this zone are located in the remnants of such meadows, where some form of management still continues.

The subalpine zone (1,200–1,450 m) is determined by the alpine timberline, which ranges from 960 to 1,405 m, average 1,243 m, depending on local conditions such as avalanche tracks and scree habitats (Treml and Banaš 2000; Treml et al. 2020). Spruce decreases gradually with altitude, forming a mix of small groups of trees and isolated specimens in the treeline ecotone zone. The subalpine zone is characterised by a shrub–grassland mosaic (Wild and Winkler 2008), dominated by clonal shrubs of *Pinus mugo* (dwarf pine), growing as *krummholz* (stunted trees), and alpine grasslands with dominating *Nardus stricta*. There are raised bogs on the flat terrain on poorly permeable subsoil.

The alpine zone (1,450–1,603 m) occurs only in a few places with the extreme conditions of the three highest summits on the Czech side. Vegetation is sparse, consisting of lichen tundra and alpine heath dominated by lichens, sedges and heather.

Pollen monitoring

Nineteen pollen traps (Table 1; Fig. 1) were installed to monitor modern pollen deposition at the sites, which were divided into three main categories according to their ecological characteristics. Above the timberline, arctic-alpine tundra sites were further divided into three groups: alpine, on the highest summits with lichen tundra where the vegetation cover is very sparse; above the treeline, a mosaic of bogs, *krummholz* stands, grasslands and isolated spruce; and within the treeline ecotone, with spruces in groups near a mosaic of *krummholz* and grassland. Below the timberline, mountain meadows in the montane zone were sampled, along with two additional sites with individual characteristics.

We used data from 23 seasons (1998–2020). However, due to external factors (including tourists, wild animals, material malfunctions and landowner restrictions), some records are missing. The number of years sampled can be seen in Table 1. The traps were sampled annually after the flowering season and processed in the laboratory following standard methods of pollen preparation. *Lycopodium* spike tablets were added to enable pollen influx calculations (Stockmarr 1971). Pollen grains were identified using atlases and keys (Punt 1976–2009; Beug 2004), as well as a reference collection at the Institute of Botany, Czech Academy of Science. A minimum of 500 terrestrial pollen grains were counted per sample when possible.

Pollen percentages were calculated from the sum of terrestrial vascular plant pollen, excluding Cyperaceae (total pollen, TP). Ericoid dwarf shrubs (*Calluna vulgaris* and *Vaccinium*-t.) were treated separately as shrubs which we classified as non-arboreal. This contradicts their arboreal nature, but agrees with their ecology because they represent treeless vegetation in the mountain environment. To characterise tree pollen deposition, we prefer arboreal pollen

Table 1 List of the 19 sites monitored in the Krkonoše

No.	Name	Site description	Group	Yrs record./ analysed	Altitude (m a.s.l.)	Lat. (50°*N*)	Long. (15°E)
1	Studniční hora	Summit plateau with lichen tundra and alpine heathland	Alpine	18/18	1,554	43′38.65″	42′24.77″
2	Vysoké kolo	Summit plateau with lichen tundra and alpine heathland	Alpine	21/20	1,496	46′35.88″	34′05.84″
3	Bílá louka	Treeless spring mire	Subalp. above TL	22/20	1,458	43′52.20″	42′17.24″
4	Harrachovy kameny	Summit plateau with alpine heathland and grassland	Subalp. above TL	21/20	1,414	45′19.47″	32′24.19″
5	Úpské rašeliniště	Open raised bog with krummholz	Subalp. above TL	19/18	1,432	44′07.81″	42′30.46″
6	Pančavská louka	Open raised bog with krummholz	Subalp. above TL	19/19	1,361	46′15.00″	32′24.08″
7	Hraniční louka	Open raised bog with krummholz and spruces	Subalp. TL ecotone	17/16	1,249	47′19.65″	30′09.87″
8	Bílé Labe	Treeless river valley	Subalp. above TL	19/19	1,386	44′14.07″	41′34.13″
9	Velká Mumlava	Spring mire with krummholz and spruces	Subalp. TL ecotone	18/18	1,302	45′45.71″	31′49.13″
10	Sněhový žlab	Rock glacial carr, steep slope	Subalp. above TL	19/18	1,382	43′56.64″	42′54.25″
11	Modrý důl	Open steep slope of glacial valley	Subalp. above TL	16/16	1,371	43′23.04″	41′48.99″
12	Schustlerova zahrádka	Spring mire in forested bottom of glacial valley	Other montane	19/19	1,034	45′49.31″	33′09.72″
13	Chalupa na Rozcestí	Spruce forest limit	Subalp. TL ecotone	22/21	1,344	42′17.50″	40′37.72″
14	Richterovy boudy	Mountain meadow	M. meadow	16/15	1,142	42′37.17″	41′56.93″
15	Severka	Mountain meadow	M. meadow	6/6	1,085	41′41.77″	42′32.86″
16	Hříběcí boudy	Mountain meadow	M. meadow	19/17	759	40′31.88″	37′53.88″
17	Vlašské boudy	Mountain meadow	M. meadow	21/20	980	40′38.76″	45′58.03″
18	Černohorské rašeliniště	Forest bog in spruce wood	Other montane	22/20	1,191	39′38.06″	45′03.94″
19	Rýchory	Mountain meadow with heathland	M. meadow	18/16	990	39′36.55″	51′11.71″

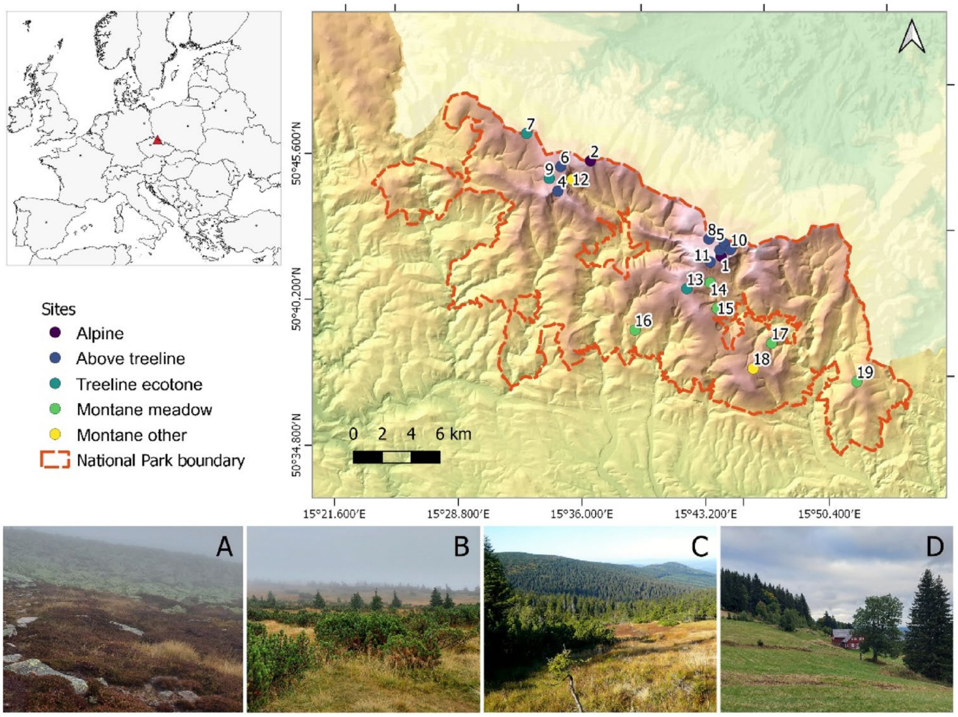


Fig. 1 Above left, location of the Krkonoše mountains; above, right, pollen trap sites within the mountain range. Below, the various zones: **A** alpine zone, summits with lichen tundra and heath; **B** subalpine zone with *krummholz* above *Picea* treeline; **C** subalpine zone within the tree line ecotone; **D** montane meadows (photos by the authors)

percentages (AP) to total pollen percentages (TP), due to the high proportion of non-arboreal pollen (NAP). This ensures comparability with other regions as well as with fossil records. Pollen accumulation rates (PARs) were calculated as arithmetical means for the monitored period.

Vegetation survey

We created a compositional model of the flora of the national park using vegetation mapped within a 5 km radius around each trap. The 0–100 m distance was mapped following the Crackles Bequest Project (Bunting et al. 2013) using the Vegetation Survey Manager in HUMPOL software (Bunting and Middleton 2005). For distances of 100–5,000 m (at 100 m intervals), cover estimates were extracted from concentric rings using GIS (von Stedingk et al. 2008). Wooded and open areas were analysed separately with special attention to communities containing sparse trees, which were evaluated according to local expert knowledge. Forest data were obtained from the KRNAP forest management plan, while open areas were rasterized from the NATURA habitat maps of the national park (Nature Conservation Agency of the Czech Republic 2011), combined with plant community data from phytosociological relevés from the Czech National Phytocenology Database (CNFD) and others available in the literature (Bercíková 1976).

Two sites lack vegetation data: site 10 due to the inaccessible steep slope of an avalanche track and site 15, due to landowner restrictions. Plant species were converted into pollen types (pollen types with the corresponding plant species are listed in Table S1) to achieve directly comparable data sets and to find whether the plant composition represented by the pollen types is sensitive enough to distinguish the position of the sites relative to the forest limit. For numerical analyses, we used vegetation within 100 m, calculating percentages from present vegetation cover using an identical procedure as for the pollen data.

Numerical analysis

Before analysing the pollen data, outlier samples were excluded to ensure data integrity. We first removed samples affected by poor pollen preservation ($n=3$), followed by filtering based on PARs to exclude extreme values outside the interquartile range, extreme high ($n=11$) and low values ($n=9$). All analyses were done with R v. 4.3.2 (R Core Team 2023) on square root transformed percentages for both pollen and vegetation, using vegan v. 2.6-8 (Oksanen et al. 2024), and indicspecies v. 1.8.0 (De Cáceres and Legendre 2009). Only taxa recorded at least at two localities were retained. We used hierarchical clustering and principal component analysis (PCA) to evaluate the pollen–vegetation relationships.

To assess whether modern pollen assemblages reflect the position of the timberline, we separately analysed a subset of sites with clear location context, based on both presence–absence and relative abundance data. The sites were categorised into the four groups (alpine, above treeline, within treeline ecotone and montane meadows (Fig. 1; Table 1). Two sites (group other montane, 12 and 18) were excluded because of their specific conditions.

To evaluate differences between sites above and below the timberline, we used PERMANOVA, a permutational multivariate analysis of variance. Similarity Percentage (SIMPER) analysis was used to identify taxa contributing most to group dissimilarity. Indicator Species Analysis (MULTIPATT) was used to detect taxa significantly associated with each group ($p < 0.05$).

Results

Over the 23 year monitoring period, 230 pollen types were recorded in the traps. The vegetation survey yielded 154 pollen types which represented plant species recorded in the KRNAP area. However, 76 taxa detected from the pollen traps were not present in the flora of the national park, which can be attributed to two main factors. The first group of taxa may have been present in the area but were overlooked during the vegetation survey, despite its thoroughness. These may include fruit or ornamental plants grown in gardens by mountain huts such as *Juglans* and *Juniperus*, as well as ruderals and plants of woodland edges or understories that can be under-represented due to the limited sensitivity of the forest management plan, such as *Ligustrum*-t., *Viburnum* and *Mercurialis perennis*. The second group consists of taxa that are not found in the KRNAP area, whose pollen probably reached the traps by long-distance transport by wind or insects. These are mostly taxa from the foothills or lowlands, such as Cerealia, *Cornus mas*, *Euonymus* and *Loranthus*. Particularly interesting is the consistent detection of *Castanea sativa*, *Olea europaea* and *Vitis vinifera*, which grow a long way away. Conversely, 26 taxa recorded in the vegetation were not present in pollen assemblages, such as *Drosera*, *Parnassia palustris*, *Maianthemum*-t. and *Tussilago farfara*-t. Both lists of absent taxa are provided in Tables S2 and S3.

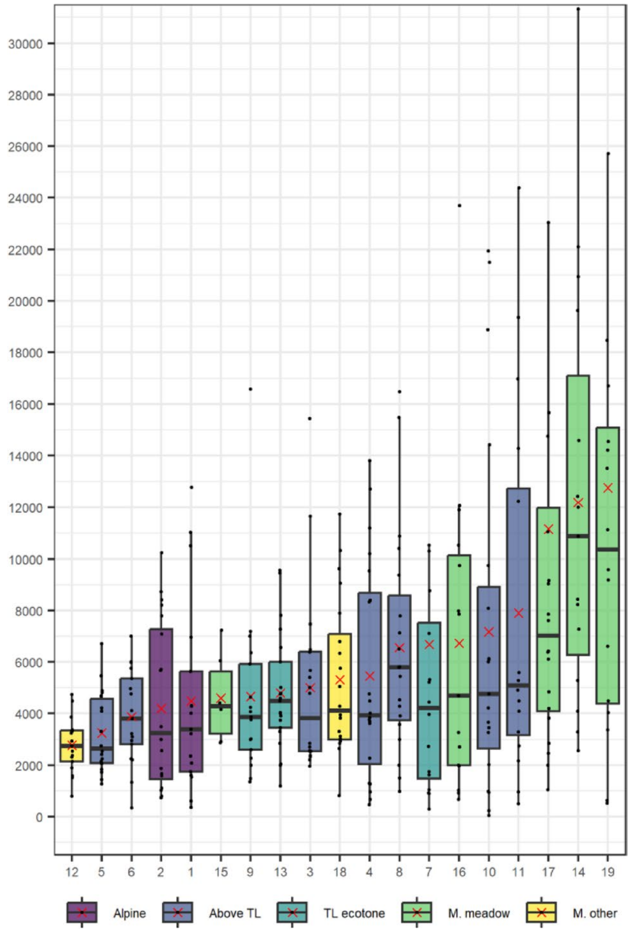


Fig. 2 Pollen accumulation rates in grains cm^{-2} year^{-1} at all sites (1–19) from 1998 to 2020 (PAR-tot), ordered by average values (red crosses). Different site groups are indicated by colours. Box plots represent interquartile ranges with medians. Abbreviations: Above TL, above treeline; TL ecoton, treeline ecotone; M, montane

Pollen accumulation rates and spatial variability

The total pollen accumulation rates for each trap (PAR-tot) show high spatial and annual variability, ranging from dozens to over 30,000 grains years^{-1} cm^{-2} (Fig. 2). Most sites recorded mean values between 4,000 and 6,500 grains years^{-1} cm^{-2}. The highest averages were found from montane meadows (sites 14, 17, 19), exceeding 10,000 grains years^{-1} cm^{-2}. The lowest averages (<4,000 grains years^{-1} cm^{-2}) were recorded from valley bottom site 12 (2,500 grains years^{-1} cm^{-2}) and from subalpine raised bogs (sites 5 and 6). One meadow site (15) displayed a notably lower PAR-tot, comparable to subalpine values, probably due to its shorter operation period (Table 1), catching only a part of inter-annual variability.

Hierarchical clustering and principle components analysis

The range of pollen records was spread over a shorter gradient (DCA1 = 1.12) compared to the vegetation records (DCA1 = 3.15), indicating greater mutual similarity among the pollen spectra. Based on the unified taxon lists of both data sets, we presume that the difference is caused mainly by the homogenising nature of pollen data, probably influenced by broader ecological factors affecting pollen dispersal.

Hierarchical clustering of vegetation data divided the sites into five groups (Fig. 3), separating bogs and alpine sites from meadows and subalpine sites. The pollen data formed six groups (Fig. 4), initially separating meadows from the subalpine and alpine sites. Key differences included: site 18,

Fig. 3 Vegetation composition (plant species given as equivalent pollen types) showing the most frequent taxa ≥ 1% of total plant cover within 100 m radius around the traps. Sites are grouped by hierarchical clustering. **I-v**: vast raised bogs, subalpine (5, 7) and montane (18) with frequent Cyperaceae, *Vaccinium* and *Pinus*; **II-v**: lichen tundra with heath (1, 2, 4), but also montane site 19 located in a heath; **III-v**: montane meadows surrounded by *Picea* forest with frequent herbs (16, 17); **IV-v**: sites close to *Picea* timberline (9 from within the treeline ecotone, and 12 and 14 from the montane zone), connected mainly by frequent occurrence of *Picea* and Poaceae; **V-v**: subalpine zone with *Pinus mugo krummholz* (3, 6, 8 and 11 above treeline and 13 within treeline ecotone)

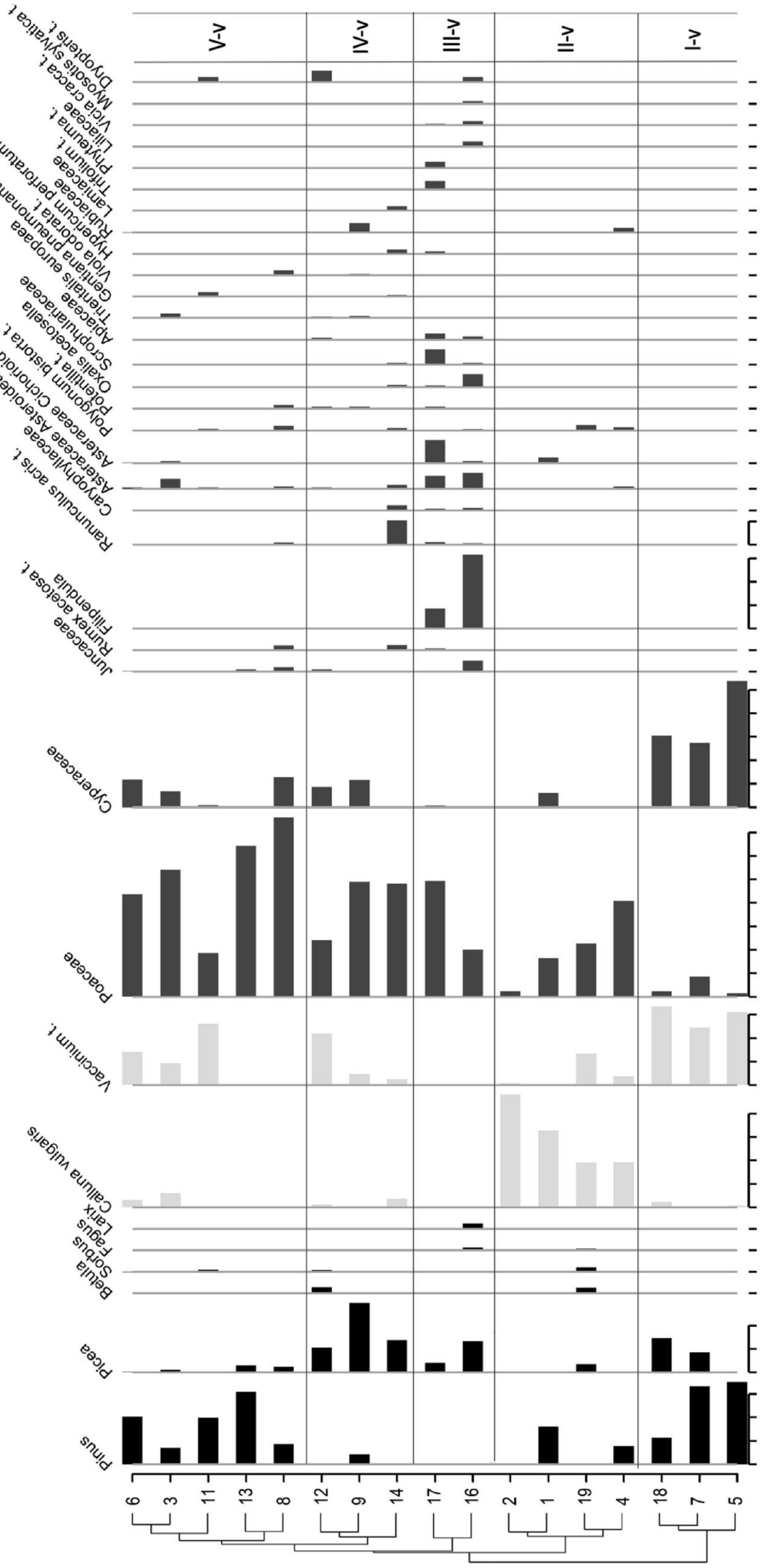
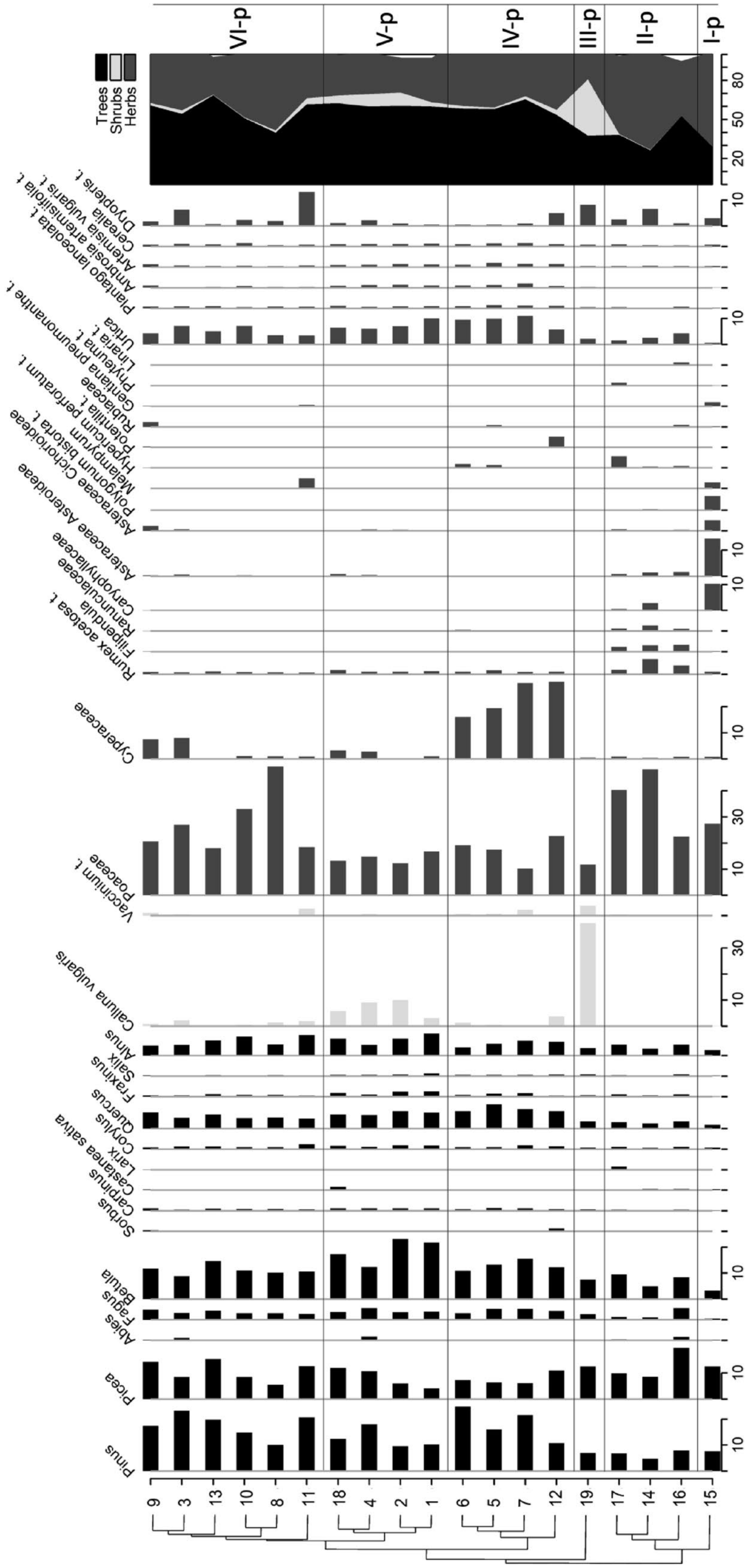


Fig. 4 Pollen percentage diagram for taxa with values ≥ 1% of the total pollen sum. On left, groups from hierarchical cluster analysis: **I-p–III-p**: montane meadows; **IV-p**: subalpine raised bogs (5, 6, 7) and montane spring mire (12); **V-p**: summit with lichen tundra and heath (1, 2, 4) and montane peat bog (18); **VI-p**: subalpine sites above the treeline (8, 10, 3) and within the treeline ecotone (9 and 13)



a montane bog, grouped with subalpine bogs in vegetation data (cluster I-v), but with alpine sites in pollen data (cluster V-p). Montane meadows (sites 14, 15, 16, 17, 19) formed distinct pollen clusters (clusters I–III-p) with sites 15 and 19 each forming a separate group, although site 19 was closer to sites above the timberline. In the vegetation data, meadows were more similar to subalpine sites. Only sites 16 and 17 separated (cluster III-v), while site 14 (cluster IV-v) was similar to site 9 within a treeline ecotone rich in *Picea* and montane glacial valley site 12. Two groups of subalpine sites, within the treeline ecotone and above the treeline, are not differentiated in either dataset.

Principal Component Analysis (Fig. 5a) further illustrates relationships between the pollen assemblages. The first axis separates regional and local influences as inferred from the taxon composition (Fig. 5b). The right-hand side corresponds to montane meadows characterised by local herb taxa (such as *Filipendula*, Ranunculaceae, *Rumex acetosa*-t., Apiaceae species, *Veronica* and *Valeriana*). Site 15 is the most distinct, forming a separate cluster in the hierarchical clustering, characterised by Asteraceae (subfam. Asteroideae, Cichorioideae), Caryophyllaceae, *Solidago* and *Polygonum bistorta*-t. Site 19 (Rýchory) is clustered together with the subalpine sites due to its high *Calluna vulgaris* values. The left side includes alpine and subalpine sites, dominated by long-distance transported tree pollen (such as *Betula*, *Quercus*, *Fagus* and *Fraxinus*) and herbs (*Urtica*, *Artemisia*, *Ambrosia*, Amaranthaceae and *Plantago lanceolata*-t.). Local components include *Pinus*, Cyperaceae and *Calluna vulgaris*.

Two montane sites (group "other montane") also grouped with sites above the timberline due to high levels of long-distance pollen: valley bottom site 12 (Schustlerova zahrádka), clustering with subalpine peatlands, and montane bog site 18 (Černohorské rašeliniště), clustering with alpine summits.

Differences between groups

PERMANOVA confirms structuring of pollen assemblages by their position relative to the timberline, based on both presence–absence and relative abundance data. No significant differences were detected between alpine and the two groups of subalpine sites; therefore, only two groups were

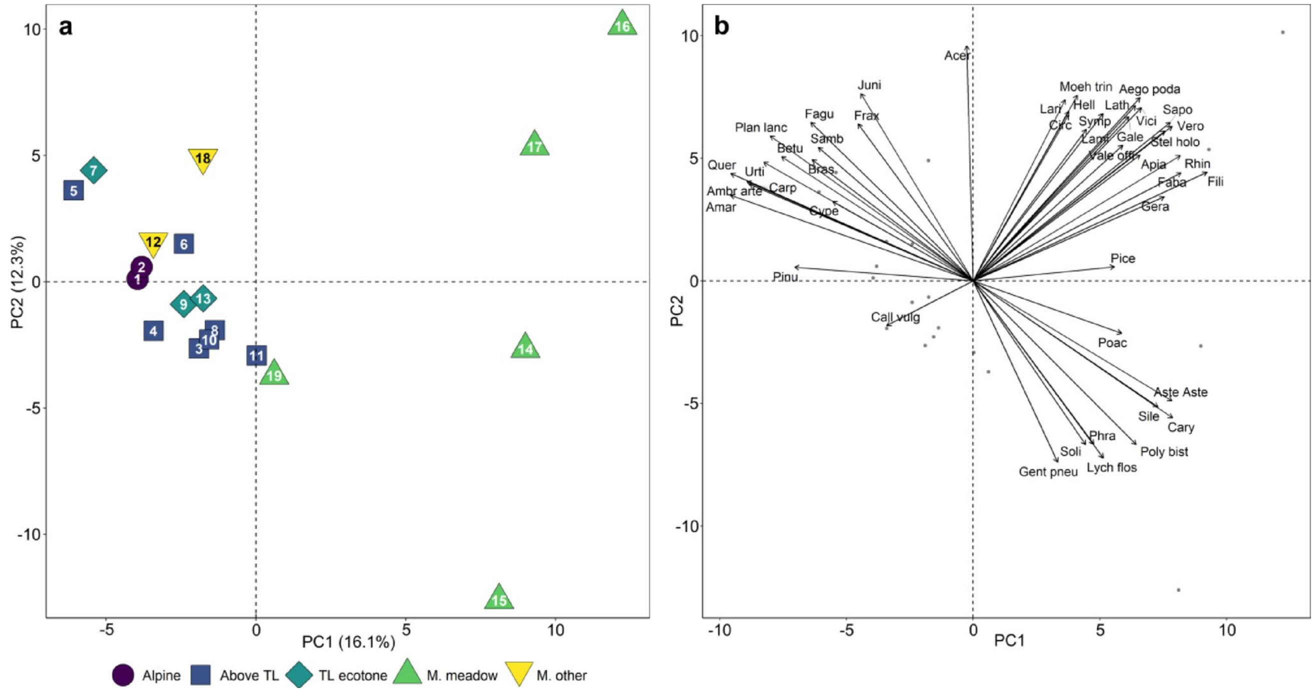


Fig. 5 Principal Component Analysis (PCA) of pollen percentage data: **a** site scores, **b** pollen type scores. The first two axes explain 28.3% of variance (Axis 1, 16.1%; Axis 2, 12.3%), The 45 taxa with the highest importance in the analysis are shown. Aego poda = *Aegopodium podagraria*, Amar = Amaranthaceae, Ambr arte = *Ambrosia artemisiifolia* t., Apia = Apiaceae, Aste Aste = Asteraceae Asteroideae, Betu = *Betula*, Bras = Brassicaceae, Call vulg = *Calluna vulgaris*, Carp = *Carpinus*, Cary = Caryophyllaceae, Circ = *Circaea*, Cype = Cyperaceae, Faba = Fabaceae, Fagu = *Fagus*, Fili = *Filipendula*, Frax = *Fraxinus*, Gale = *Galeopsis*/*Ballota* t., Gent pneu = *Gentiana pneumonanthe* t., Gera = *Geranium*, Hell = *Helleborus*, Juni = *Juniperus*, Lami = Lamiaceae, Lari = *Larix*, Lath = *Lathyrus*, Lych flos = *Lychnis flos cuculi* t., Moeh trin = *Moehringia trinervia* t., Phra = *Phragmites*, Pice = *Picea*, Pinu = *Pinus*, Plan lanc = *Plantago lanceolata* t., Poac = Poaceae, Poly bist = *Polygonum bistorta* t., Quer = *Quercus*, Rhin = *Rhinanthus* t., Samb = *Sambucus*, Sapo = *Saponaria*, Sile = Silenaceae, Soli = *Aster tripolium* t,, Stel holo = *Stellaria holostea* t., Symp = *Symphytum*, Urti = *Urtica*, Vale offi = *Valeriana officinalis* t., Vero = *Veronica* t., Vici = *Vicia* t

further compared, those above and below the timberline. PERMANOVA on presence–absence data explains only 9.9% of the variation, whereas the analysis based on relative abundance data explains a much higher proportion (29.5%). Additionally, F values indicate more distinct separation in relative abundance data (F = 6.27) than in presence–absence data (F = 1.63). These results suggest that differences in taxa dominance, rather than in overall composition, play a key role in distinguishing assemblages on either side of the forest limit.

The main taxa driving the separation of relative abundance data (Fig. 6a) are among the most frequent in the pollen spectra and correspond well with the PCA results. The group above the timberline is characterised by local *Pinus* and Cyperaceae, followed by taxa of long-distance origin. The group below it is dominated by herbaceous meadow taxa, along with the trees *Picea* and *Larix*. In contrast, presence–absence data revealed different contributing taxa (Fig. 6b), which are rare in the pollen spectra. Again, a pattern of long-distance origin is valid for the above group, as it includes many non-local taxa. These pollen types come from the closer montane zone (*Acer*, *Larix*), but also from further away in the lowlands (such as *Sambucus*, *Populus*, *Syringa* and *Vitis*). Local arctic-alpine tundra taxa also contributed, such as *Oxycoccus palustris*, *Trientalis europaea*, *Aconitum*-t., *Senecio*-t. (representing *S. nemorensis* or *S. hercynicus*), Liliaceae (including the frequent *Veratrum album*) and *Gentiana pneumonanthe*-t. However, none of these pollen types are exclusive to the tundra, as all of them can also be found in montane meadows. Only *Lychnis flos-cuculi*-t., *Anemone nemorosa*-t. and *Leucojum*-t. occur exclusively in montane meadows and they may serve as indicators for this habitat.

Below the timberline in general, only a few contributing taxa are not locally present (Figs. 6a, b). Even the taxa which are considered non-local based on our vegetation survey may still occur near montane meadows. This is particularly true for *Polygonum aviculare*-t., *Mercurialis perennis*, *Sedum* and *Centaurea cyanus* (possibly referable to *C. montana*). *Genista*-t. pollen, the highest contributor in presence–absence data, probably originates from the invasive *Lupinus polyphyllus*, which is spreading in the Krkonoše.

Indicator Species Analysis based on relative abundances identified 44 significant taxa ($p < 0.01$), 18 above the timberline (for example, Cyperaceae, *Sambucus*, *Ambrosia*, Amaranthaceae, *Pinus*, *Betula*, *Urtica* and *Quercus*) and 26 below it (such as *Filipendula*, *Genista*, *Caltha palustris*-t. and *Rumex acetosa*-t.). Analysis of presence–absence data revealed far fewer indicators: two above the forest (*Oxycoccus palustris* and *Ligustrum*-t.) and four below (Fabaceae, *Veronica*-t., *Phragmites* and *Silene*). However, none of these is exclusive to zones above or below the timberline. A full list of significant indicator taxa, and taxa contributing most to the observed differences between the groups with corresponding statistical results is provided in Tables S4–S6.

Site-specific pollen assemblages

Several sites showed some degree of individuality in their pollen assemblages, which we believe should be further described here:

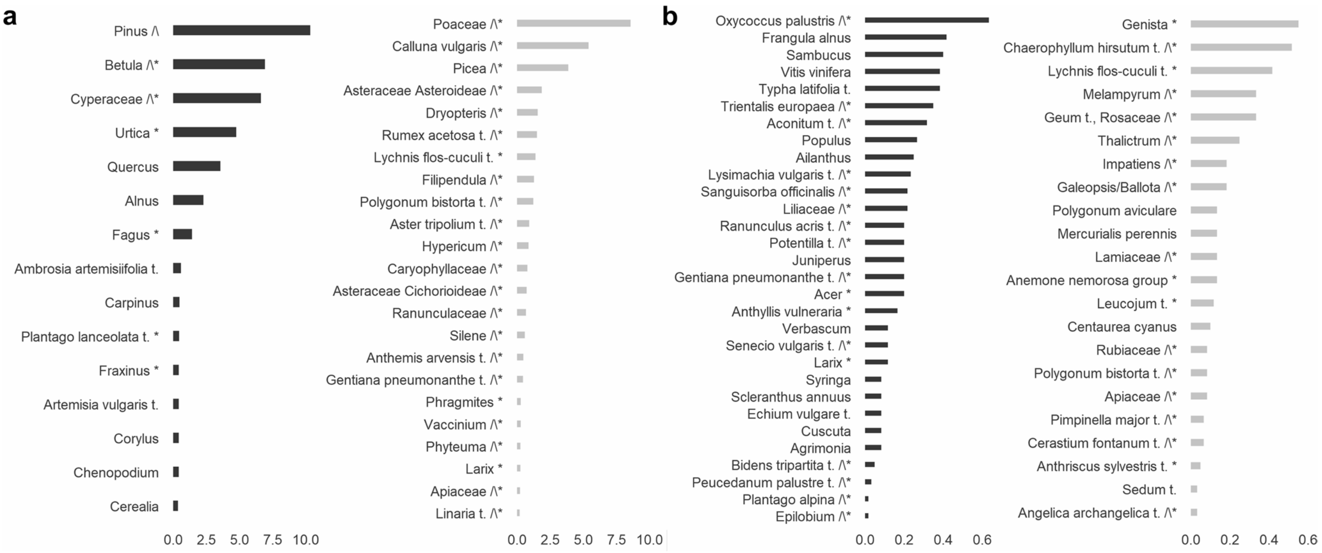


Fig. 6 Pollen types contributing most to the differences between the groups above and below the timberline (SIMPER analysis), ranked by their average contribution (the length of bars). Together these taxa explain 70% of the difference. **a** abundance data; **b** presence–absence data. Above the timberline – dark bars; below it – light bars. Species indications: * local below; /\ local above; */\ local both below and above

Site 4 Harrachovy kameny, is an alpine summit plateau with heath, but differing from sites 1 and 2 by its large alpine grassland cover. It clusters with the alpine sites in both pollen and vegetation data, primarily due to high *Calluna vulgaris* values. Nevertheless, we categorise it as a subalpine site, which better reflects its local conditions.

Mountain meadow site 15 Severka clusters as a single-site group, notably rich in meadow taxa. This aligns with its species rich vegetation composition, as previously documented here by Krahulec et al. (1997) and Pecháčková and Krahulec (1995). A local vegetation survey was not possible, limiting direct comparison with other meadow sites.

Mountain meadow site 19 Rýchory shows exceptionally high values of *Calluna vulgaris*, distorting percentage relationships. Therefore, this site was excluded from percentage analyses but retained for PAR calculations.

Subalpine site 8 Bílé Labe shows high Poaceae and NAP and relatively low *Pinus* values compared to other subalpine sites (Fig. 4). This pollen composition reflects its wind-exposed river valley location with a high influx to the trap from local grasses.

Site 12 Schustlerova zahrádka, located in a deep valley, clustered with subalpine sites, despite its montane position. This spectrum agrees with AO systems classifying this valley as leeward (downwind), where wind currents collect pollen from plains higher up and deposit it into this valley bottom below. Here, *Pinus* and long-distance transported taxa dominate, while the local *Picea* forest is under-represented.

Site 18 Černohorské rašeliniště, a wooded raised bog on a mountain saddle, clustered with alpine sites. The pollen spectra are very similar, with a high proportion of long-distance transported pollen types, making the local *Pinus mugo* shrubs and nearby *Picea* dominated forest hard to detect. Proportions of these taxa, as well as those of *Quercus*, *Corylus*, *Alnus*, *Urtica*, *Ambrosia* and *Artemisia*, further support the strong influence of regional pollen transport at this site.

Presence thresholds and taxon responses across timberline gradients

Pollen values of the main taxa differ according to their position relative to the timberline (Fig. 7). Although numerical analyses showed alpine and subalpine sites to be similar, some differences are still apparent. Alpine sites, despite the absence of pollinating trees within several hundred metres, show the highest *Betula* values (1,000 grains cm^{-2} $year^{-1}$ and 35% AP, compared to 500 grains cm^{-2} $year^{-1}$ and 20% AP in subalpine sites). *Pinus*, *Quercus* and *Alnus* are relatively balanced across the alpine sites (~400 grains cm^{-2} $year^{-1}$ and 10–15% AP). *Picea* shows the lowest values of all the groups (200 grains cm^{-2} $year^{-1}$ and ~7% AP). Locally growing *Calluna vulgaris* is typical for this zone (~300 grains cm^{-2} $year^{-1}$ and 5% AP).

Subalpine sites are characterised by higher *Pinus* and *Picea* values compared to alpine sites. *Pinus* reaches its peak, originating from local *krummholz* stands (~1,000 grains cm^{-2} $year^{-1}$ and ~30–40% AP). *Picea* averages 500 grains cm^{-2} $year^{-1}$ and 18% AP. Other tree pollen values are similar to those found in the alpine zone. Sites within the treeline ecotone differed from the sites above the timber line by their lower NAP (averages of 40 vs. 30%) and higher AP (averages of 65 vs. 55%) values.

Montane meadows display the highest values of *Picea* (~ 800 grains cm^{-2} $year^{-1}$ and 30% AP) and Poaceae (2,800 grains cm^{-2} $year^{-1}$, ~35% TP), along with the lowest AP proportions (average ~50%). Scattered beech trees nearby do not significantly increase *Fagus* pollen values beyond those recorded elsewhere.

Trees

Local occurrence (~ 100 m or within respective vegetation zone) generally corresponds to the highest pollen values (indicated by shaded cells and bold text in Table 2). Comparisons across zones and sites allowed us to determine presence/absence thresholds for key pollen taxa. Regional deposition values, considered absence thresholds under present conditions, are listed in Table 3. Taxa absent from the vegetation of either zone but showing similar pollen proportions across all sites are considered to represent background pollen deposition (Sugita 1994). Differences in PARs between zones are sometimes less distinct than in percentages, mainly due to strong variations of PAR-tot across site types (Fig. 2). We emphasise arboreal percentages (AP) over total percentages (TP) to account for site-specific variation in non-arboreal pollen components.

Pinus dominates in the subalpine zone (450–1,300 grains cm^{-2} $year^{-1}$). However, these values are not much different from those of the meadows a long way from the timberline, receiving only regional input (300–400 grains cm^{-2} $year^{-1}$), while meadows closer to the timberline exceed 500 grains cm^{-2} $year^{-1}$. The high *Pinus* background pollen deposition indicate that local presence should be convincingly indicated by even higher values, exceeding 600 grains cm^{-2} $year^{-1}$. The percentage threshold for local presence is ~ 30% AP (15% TP).

Picea peaks in meadows (600–1,200 grains cm^{-2} $year^{-1}$), and these values represent spruce forest within ~ 40 m. The lower range overlaps with the treeline ecotone sites 9 and 13 (600–800 grains cm^{-2} $year^{-1}$). A value of ~ 600 grains cm^{-2} $year^{-1}$ can be inferred as a threshold for lower local presence, and percentage thresholds are > 20% AP (10–15% TP).

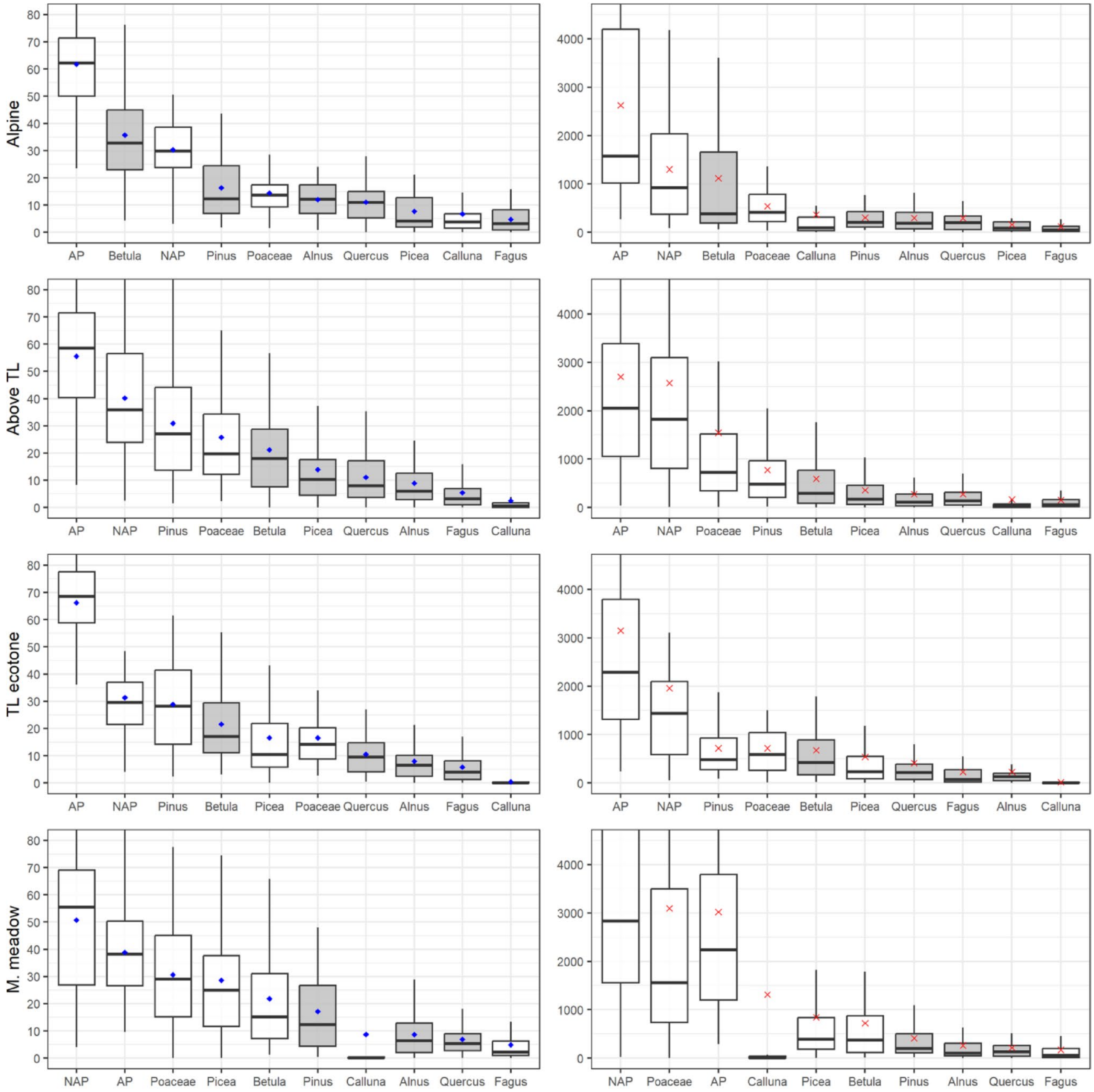


Fig. 7 Values of the main pollen types in each group of sites. Plant species absent from a particular zone are shown in grey. Left, tree pollen percentages (from AP sum). Right, pollen accumulation rates (pollen grains cm^{-2} year^{-1}). Blue dots and red crosses show arithmetical means for all years. Included sites: Alpine 1, 2; Above TL 3–6, 8, 10–11, TL ecotone 7, 9, 13; Montane meadow 14–17 (also 19 for PAR). Sites 12 and 18 were excluded due to their intermediate locations. Box plots represent interquartile ranges with medians (not visible, M. meadow PAR 3rd interquartile range = 6,700)

Fagus grows locally in two meadows (sites 16 and 19), with scattered trees around the traps (350 grains cm^{-2} year^{-1} and 9% AP, 4.5% TP), representing thresholds for low local presence. However, subalpine sites show similar values, making it difficult to distinguish low local occurrence from the regional background.

Similarly, *Abies* shows little variation across the traps, with values ranging 2–120 grains cm^{-2} year^{-1} and 0.2–1.9% AP (0.2–1.7% TP), and its local presence at one site is not reflected by higher values. Below the forest limit, the degree of horizontal transport seems to be limited as shown by absolute minima of *Abies* and *Fagus* at those montane sites where they are absent.

Table 2 Pollen values for key taxa locally present in each zone. The highest values are marked in bold. TL, treeline. Percentages are either from the arboreal pollen sum (AP) or from the total pollen sum (TP)

Local occurrence	Alpine zone on summits, lichen tundra	Subalpine zone, areas above TL and diffused TL ecotone	Montane zone meadows
PINUS, mainly *P. mugo* (*krummholz* species) and *P. sylvestris* (sporadic in foothills)	Scattered shrubs 260–360 grains cm^{-2} year^{-1} 16% AP (10% TP)	Local *krummholz* **450–1,300 grains cm^{-2} year^{-1}** **27–42% AP** (15–25% TP)	Not present 600–800 m away (sites 14,15): 330–**570** grains cm^{-2} year^{-1} 19–**29**% AP (5–8% TP) 5 km away (sites 16, 17, 19): 300–400 grains cm^{-2} year^{-1} 14–17% AP (7–8% TP)
PICEA, dominating forest species	Not producing pollen 120–200 grains cm^{-2} year^{-1} 6–9% AP (4–6% TP)	Only occasionally or not producing pollen **sites 9, 11, 13** **600–800 grains cm^{-2} year^{-1}** **~20% AP (13–15% TP)** sites 3, 4, 5, 6, 7, 8, 10 170–490 grains cm^{-2} year^{-1} 10–14% AP (5–11% TP)	Forest surrounding the meadow openings **600–1,200 grains cm^{-2} year^{-1}** **23–40% AP** (9–20% TP)
FAGUS, in mixed (sub)montane woods with *Picea* and scattered *Acer*	Not present (first trees > 1 km away) ~100–**300** grains cm^{-2} year^{-1} 4–7% AP (2–4% TP)		Local specimens, continue into near forest (sites 16, 19): **350 grains cm^{-2} year^{-1}** **~9% AP** (4.5% TP) 200–600 m away (sites 14, 15, 17, 18): 20–160 grains cm^{-2} year^{-1} 1.5–4% AP (0.5–3% TP)
ABIES, low regional occurrence	Not present (first trees > 1.5 km away) **2–100 grains cm^{-2} year^{-1}** (most often ~10) **0.2–1.9% AP** (0.1–1.4% TP)		400 m away (sites 12, 16, 17) local at site 14 **5–20 grains cm^{-2} year^{-1}** **0.2–0.5% AP** (0.2–0.5% TP) but site 16: **120 grains cm^{-2} year^{-1}, 1.3% AP** (1.7% TP)
BETULA, *B. carpatica*, *B. pendula* on valley slopes (rather sporadic). In the foothills *B. pubescens*	Not present **1,000 grains cm^{-2} year^{-1}** **35% AP (22% TP)**	Sporadically present ~500 grains cm^{-2} year^{-1}, 16–27% AP (9–15% TP)	Local at sites 18 and 19: **1,000 grains cm^{-2} year^{-1}** **28% AP (8–17% TP)** otherwise > 200 m away: ~500 grains cm^{-2} year^{-1}, 10–25% AP (3–10% TP)
NAP	28–35%	27–48%	46–73%
CALLUNA	If not present: 0 **550–750 grains cm^{-2} year^{-1}** **10% TP**	50–320 grains cm^{-2} year^{-1} 1–5.5% TP	Heath (site 19): 6,000 grains cm^{-2} year^{-1}, 40% TP
VACCINIUM	Extensive cover (sites 7, 9, 11, 19): 130–350 grains cm^{-2} year^{-1}, 1–4% TP; if not present: 0		
POACEAE	Sites 8, 14, 17: 4,000– 6,000 grains cm^{-2} year^{-1}, 40–50%; other sites: 10–33%		
CYPERACEAE	Locally on peatlands (sites 5, 6, 7, 12): 420–1,400 grains cm^{-2} year^{-1}, 16–30% TP		

Betula peaks in alpine sites and in the montane meadows near birch stands (both 1,000 grains cm^{-2} year^{-1} and ~30% AP). In the subalpine zone and in meadows without local *Betula*, values were about half.

Quercus and *Corylus* are actually absent from the vegetation of the national park, but they can be found in the foothills. *Alnus* grows in some parts of the montane zone, but no closer than 200 m from our meadows. All three trees show consistently low pollen values that are slightly higher in the alpine zone, representing regional pollen deposition (Table 3). *Acer* and *Fraxinus* grow sporadically in some montane to sub-montane regions. *Acer* pollen values are mostly negligible. *Fraxinus* in the alpine zone reaches 3% AP and in meadows ~2% AP (sites 18 and 19).

Herbs and Dwarf shrubs

NAP is quite high across all sites (~30–70%), lowest above the timberline (30–40%) and highest in the meadows (50–70%). Poaceae peaks in open sites (4,000–6,000 grains cm^{-2} year^{-1} and 40–50%) such as subalpine site 8 Bílé Labe and meadows 14 Richtrovy b. and 17 Hříběcí b. Elsewhere, values are 500–2,400 grains cm^{-2} year^{-1} and 10–33%, varying

Table 3 Regional pollen deposition values (pollen background) at our sites in the Krkonoše inferred from presence/absence of these taxa. Mean values are given after the slashes.

Pollen taxon	PAR (grains cm^{-2} $year^{-1}$)	% AP	% TP	Included sites
Pinus	300–400/**370**	14–16.5/**15**	7–8/**7.4**	16, 17, 19
Picea	120–200/**160**	6.5–8.5/**7.5**	4–6/**5**	1, 2
Fagus	95–280/ **165**	3.5–7.5/**5.5**	2.2–4.5/**3**	all but 12, 14–17, 19
Abies	2–100/**15**	0.2–1.9/**0.53**	0.1–1.4	all but 16 and 17
Quercus	50–720/**270**	6–16/ **10**	1.5–9.5/**5**	all
Betula	400–1000/**700**	16–37/**24**	9–23/**13.5**	1–11
Alnus	80–500/ **260**	8–14/**9**	3–8.5/**5**	all
Corylus	20–115/**50**	1.2–2.5/**1.7**	0.5–1.9/**1**	all
Cerealia	20–65/**38**		0.5–1.4/**0.8**	all
Urtica	120–550/**300**		0.7–10/**5.7**	all

across sites, which seem to reflect local vegetation. Their wide occurrence makes background estimates difficult.

Calluna cover is prominent on the summits (2 Studniční hora, 4 Harrachovy kameny) with 550–750 grains cm^{-2} $year^{-1}$ and 10%. The highest value is typical for site 19 Rýchory, where a *Calluna* heath yielded 6,000 grains cm^{-2} $year^{-1}$ and ~40% TP. Sites with lower *Calluna* presence range from 50 to 320 grains cm^{-2} $year^{-1}$ and 1–5.5%.

Vaccinium-t. (represented by *V. myrtillus*, *V. oxycoccos* and *V. uliginosum*) is generally low (~25 grains cm^{-2} $year^{-1}$ and 0.5%), even where locally abundant. Higher values (1–4% and 130–350 grains cm^{-2} $year^{-1}$) occur only at sites with dense and extensive coverage (7 Hraniční louka, 9 Velká Mumlava, 11 Modrý důl, 19 Rýchory).

Cyperaceae are high in bogs and wetland sites (5, 6, 7, 12), with 420–1,400 grains cm^{-2} $year^{-1}$ and 16–30%, well reflecting local conditions. In the alpine zone, the values are much lower (10–50 grains cm^{-2} $year^{-1}$ and < 8%), indicating their limited long-distance transport.

Cerealia pollen (including *Secale* due to low values of all Cerealia pollen types) is present in small amounts at all sites (20–65 grains cm^{-2} $year^{-1}$ <1.4%). Therefore, this pollen type has been transported over long distances from cornfields in the lowlands, but only in limited quantity. Sites above the timberline show slightly higher values, as the 1% threshold is crossed more often there.

Other anthropogenic indicators reaching the 1% threshold are *Artemisia*, *Plantago lanceolata*-t., *Urtica* and *Rumex acetosa*-t. Identical patterns are shown by *Artemisia* and *Plantago lanceolata*-t. (60/70 grains cm^{-2} $year^{-1}$ and ~1%), slightly higher above the forest limit. *Urtica* values are generally higher (Table 3). *Rumex acetosa*-t. is locally abundant in meadows and also in pollen (for example, 650 grains cm^{-2} $year^{-1}$ and 5% at site 14; 250 grains cm^{-2} $year^{-1}$ and ~3% at site 16).

Discussion

Pollen assemblages and the timberline

Our results confirm that the position of sites relative to the timberline significantly influences modern pollen assemblages, clearly distinguishing the arctic-alpine tundra of the Krkonoše mountains (alpine and subalpine zone) from montane meadows. Tundra sites are characterised by a marked presence of pollen types from species absent from the local vegetation, along with increased representations of local *Pinus* and *Calluna vulgaris*. The high proportion of background pollen suggests that strong wind transport is the dominant factor affecting pollen deposition above the timberline. On alpine summits, this updraught effect is particularly pronounced, probably due to the scarcity of local vegetation, as already observed in empirical studies (Gaillard et al. 1992; Hicks 1994; Hjelle 1999; Bunting 2003; Mazier et al. 2006; Seppä and Hicks 2006). In contrast, pollen assemblages from montane meadows show reduced influence of long-distance pollen input and are instead characterised by the presence of local taxa. Compared to the Pyrenees, where updraught effects were similarly strong above and below the timberline (Cañellas-Boltà et al. 2009), our results show the unique role of anemo-orographic systems in the Krkonoše in increasing the differentiation between site groups.

The background pollen includes the full regional tree species pool, from local dominants (*Pinus* and *Picea*) to taxa originating in distant montane to submontane zones. These include arboreal taxa (*Betula*, *Alnus*, *Fagus*, *Quercus*, *Abies* and *Corylus*), and low but consistent occurrences of herbaceous pollen types, mainly wind pollinated, such as *Urtica*, *Ambrosia*, *Artemisia*, *Plantago lanceolata*-t., *Rumex acetosa*-t. and Cerealia. In contrast to our findings, Bjune (2014) suggested that *Urtica* pollen indicates local nettle populations and is not transported over long distances. Such taxa, often used to indicate human activities (Gaillard 2013), require careful interpretation in fossil records as previously emphasised (Mazier et al. 2006). Their mere presence does not imply local disturbances unless supported by significantly raised values, especially in mountain ecosystems, where distinguishing local from regional pollen signals is essential.

Montane meadows, open areas of secondary treeless habitats in the forest, show strong contributions of local taxa, particularly Poaceae and other herbs such as Asteraceae, Ranunculaceae, Caryophylaceae, *Rumex acetosa*-t., *Filipendula* and *Hypericum perforatum*-t. The dominance of Poaceae supports earlier findings that suggest their local origin (Hjelle 1999; van der Knaap et al. 2001; Bunting 2003; Mazier et al. 2006; López-Sáez et al. 2018; Fontana et al. 2023). Although the Poaceae pollen signal can be complex due to the many species within it and the influence of management practices on flowering (Sjögren et al. 2015), our results support its use as an approximate indicator of the degree of openness around a site.

Montane meadows also show the highest ranges of NAP values (46–73%), despite being close to the forests which dominate the montane zone, as the diameters of forest openings are 120–300 m. These values suggest that their source area is small and local. This is not exceptional, as a similar pattern has already been observed by Hicks (2006) in climatically exposed areas and also recently by Prach et al. (2023) who reported a strong local pollen signal and poor representation of trees from openings in taiga forest. Therefore, when interpreting pollen spectra with high NAP values, the nearby presence of dense forests cannot be ruled out.

Slight over-representation of NAP pollen in pollen traps may also influence the detection of forest, as has been documented by studies comparing results from pollen traps with moss polsters or lake sediments (Räsänen et al. 2004; Lisitsyna et al. 2012; Lisitsyna and Hicks 2014) and this may also apply to the Krkonoše. We did not have sites in smaller forest openings that would have represented the local forest pollen signal better (Calcote 1995), limiting direct comparisons with meadows.

Surprisingly, the tundra sites had high AP values (40–66%), because arboreal pollen dominates the background signal. This underestimates the degree of openness indicated by AP/NAP ratios. This phenomenon has also been demonstrated by studies of pollen and vegetation in the Alps and Norway (Pardoe 2001; Court-Picon et al. 2005), reinforcing the assumption that raw AP/NAP ratios are not reliable indicators of landscape openness in regions influenced by long-distance pollen input (Sugita et al. 1999; Broström et al. 2004; Mazier et al. 2006).

We attempted to identify pollen indicator taxa for areas above and below the timberline, but this was mostly unsuccessful as most pollen types identified from their plant species were present both above and below the forest limit. It was also reflected in the poor separation of the hierarchical clustering of vegetation data in pollen types. Only *Lychnis flos-cuculi*, *Anemone nemorosa*-t. and *Leucojum*-t. emerged as possible indicators of areas below the timberline, being restricted to those areas both in pollen and vegetation data. Interestingly, the pollen records of herbs quite faithfully reflected their presence in the vegetation above or below the timberline, with the exception of the wind-pollinated taxa discussed above.

Relationships between pollen and vegetation

Elevation has often been identified as the primary gradient shaping pollen–vegetation relationships (for example, Court-Picon et al. 2005; Cañellas-Boltà et al. 2009; Boutahar et al. 2023; Fontana et al. 2023). However, in the Krkonoše, pollen transport factors that are specific to each site play a larger role than height alone. Although it is still one of the main contributing factors behind the gradient, since higher sites have stronger updraughts, some lower sites are also strongly influenced by input of long distance pollen, thus diverging from the expected pattern. One such site is a montane forest bog at Černá hora saddle (site 18), whose assemblages resemble those of the alpine zone. Another is a spring mire in the Labský důl valley (site 12, Schustlerova zahrádka), clustering with subalpine peat bogs. In both cases, their pollen spectra poorly reflect the spruce forests nearby.

Hierarchical clustering of pollen data separates sites above and below the timberline more clearly than vegetation data. The pollen types identified from the vegetation show higher variability between the sites (also noted by Felde et al. 2014), making the distinction of the forest limit less apparent. Raised bogs exhibit distinct patterns in both datasets. They are defined by high Cyperaceae pollen values that reliably reflect their local presence in the vegetation. This finding is consistent with previous studies (Hjelle 1999; van der Knaap et al. 2001; Bunting 2003; Mazier et al. 2006; López-Sáez et al. 2018). The alpine zone is characterised in both datasets by prominent *Calluna* values, indicating heather as a local pollen source (Bunting 2003; Pardoe 2006; though not Court-Picon et al. 2006). *Vaccinium*, although frequent in the subalpine zone, is strongly underrepresented in modern pollen assemblages, which was also noted by Mazier et al. (2006) in the Pyrenees and Prach et al. (2023) in northern Siberia. Our results strongly emphasise that even minimal pollen presence should not merely be seen as a trace signal, but rather as clear evidence of substantial local populations.

Pollen accumulation rates and biomass

Spatial and annual variability in average total PAR at each site (PAR-tot) is substantial, yet consistent with other pollen monitoring studies at plant distribution limits (for example, Hicks 2001; van der Knaap et al. 2001; Bjune 2014; Tonkov et al. 2016). This highlights the importance of long-term datasets for achieving robust averages for interpretations (Hicks 1994, 2001). Therefore, spatial variability in PARs is influenced not only by the representation of taxa in the vegetation but also by marked differences in PAR-tot values across sites. Under these circumstances, pollen percentages appear to be a more reliable metric for comparisons across different altitudinal zones and habitat types, particularly those based on the arboreal pollen sum, which tend to have a more stable pattern than PARs.

A linear relationship between PARs and local vegetation biomass is generally assumed (Seppä et al. 2009; Sugita et al. 2010; Matthias and Giesecke 2014; Knight et al. 2021). In the Krkonoše, we can also infer this pattern across groups and habitat types. Sites with high biomass production, such as montane meadows (sites 14, 17, 19) show the highest PAR-tot values, whereas low biomass sites, such as subalpine raised bogs (sites 5, 6) or summits (sites 1, 2), have the lowest values. Pollen influx therefore declines with increasing elevation or habitat severity, consistent with findings from other regions (van der Knaap et al. 2001; Birks and Bjune 2010; Bjune 2014).

Additionally, low PAR-tot values in the Krkonoše are often accompanied by a high input of background pollen, suggesting an inverse relationship between local biomass and background pollen deposition. In other words, low local pollen productivity is compensated by pollen from long-distance transport (Giesecke et al. 2014). Two findings in particular support this relationship: first, the low rates of background pollen in montane meadows with considerably higher biomass than other sites; and second, a specific example of how pollen spectra can be affected by local conditions is given by site 12 (Schustlerova zahrádka in the Labský důl valley), which has the lowest pollen influx but high rates of background pollen, resembling tundra sites. However, this may reflect the mostly young (~20 years) surrounding forests, still with low pollen production, leading to an underestimation of potential biomass reflected by the pollen values (Matthias et al. 2012), since spruce requires several decades to reach maturity in terms of pollen and seed production (Viglas et al. 2013; Splawinski et al. 2022). Longer monitoring would be needed to discover whether this pattern persists or if it changes as the trees mature.

Pollen threshold values: alpine and boreal forest limits

In the Krkonoše, PAR values are generally low, reaching maxima of 1,300 grains cm^{-2} year^{-1} of *Pinus* in the subalpine zone and 1,200 grains cm^{-2} year^{-1} of *Picea* in the montane meadows. Low pollen production seems to be typical for plants growing near their physiological limits, as repeatedly reported from other climatically exposed areas (Markgraf 1980; van der Knaap et al. 2001, 2010; Hicks 2006; Huusko and Hicks 2009; Abraham et al. 2021).

Our findings demonstrate that the presence/absence thresholds for *Pinus* and *Betula* match those from well-studied treeline ecotones in both boreal Fennoscandia (Hicks 1994, 2001; Hicks and Hyvärinen 1999; Seppä and Hicks 2006) and the Alps (van der Knaap et al. 2001), showing the robustness of these indicators in different mountain systems. For *Pinus*, the threshold in the Krkonoše is 370 grains cm^{-2} year^{-1}, similar to that in the Alps (243–560 grains cm^{-2} year^{-1} within three monitored regions), and <500 grains cm^{-2} year^{-1} in Fennoscandia. *Betula* thresholds are more variable across the Krkonoše sites, but with exception of the alpine sites where its pollen dominates, birch does not greatly exceed 500 grains cm^{-2} year^{-1} in any of the three regions (500 grains cm^{-2} year^{-1} in Fennoscandia and 139–574 grains cm^{-2} year^{-1} in the Alps).

Picea PARs are higher in the Krkonoše than in Fennoscandia, although only by one order of magnitude (160 grains cm^{-2} year^{-1} vs. 40 grains cm^{-2} year^{-1} in Fennoscandia), but in the Alps they are even higher (243–560 grains cm^{-2} year^{-1}). The regional deposition of *Alnus* is similar both in the Krkonoše and in the Alps with ranges of 80–500 grains cm^{-2} year^{-1}, but very low in Fennoscandia where alder is also present at the treeline, with only a few grains cm^{-2} year^{-1} (Birks and Bjune 2010). In the case of Krkonoše, the local presence of *Pinus* and *Picea* at their distribution limit can explain their similar threshold values to those in Fennoscandia. The differences in the values of *Betula* and *Alnus* between these regions could be because they mainly grow at lower altitudes in the Krkonoše where their pollen production might be significantly higher than in Fennoscandia. Although *Betula* thresholds are similar across the three regions, birch is much more frequent near the woodland limit in Fennoscandia, meaning that its lower pollen production there is counterbalanced by denser stands. This indicates that pollen production by local trees at their distribution limits is broadly comparable between the Krkonoše forest limit and the boreal treeline, demonstrating wider geo-ecological similarities between the two regions, including pollen output.

Pollen threshold values for the key taxa

Pinus dominates the subalpine zone in the Krkonoše, both in terms of vegetation and pollen. However, its dominance in pollen is not overwhelming, and values above and below the timberline partially overlap. This may be attributed to the exceptionally good dispersal capacity of *Pinus* pollen, which has also been found in other mountain regions (Court-Picon et al. 2005, 2006; Cañellas-Boltà et al. 2009; Sánchez-Morales et al. 2025). Another factor that contributes to the overlapping values could be the mixed origins of *Pinus* pollen, probably from both *P. mugo* at its distribution limit in years of extreme pollen production, and *P. sylvestris*, occurring rather sporadically lower down in foothills, but producing relatively high and stable quantities of pollen. We believe that our dataset, covering 23 pollen seasons, is sufficiently robust to capture possible variations in pollen production. Therefore, we recommend interpreting the higher range of the recorded values as being indicative of local occurrence. Interestingly, even subalpine sites with dense *krummholz* stands did not have distinctly higher pollen values, further supporting the strong dispersal ability of pine pollen and efficient mixing above the forest limit.

Picea forms the diffuse alpine timberline and is by far the most frequent tree growing in the montane zone. Its highest pollen values are recorded from the montane meadows, but they are not substantially different from other sites within the treeline ecotone. This can be caused by the fact that even above the forest limit, *Picea* can occasionally produce pollen in climatically favourable years, although it mainly reproduces vegetatively (Šenfeldr and Maděra 2011). Lower *Picea* values from the traps above the treeline support the interpretation that the local presence of spruce is reasonably well reflected in the pollen record. While *Picea* forests surrounding montane meadows do not dominate the pollen spectra as might be expected, they provide a good reflection of forest openings in the pollen records from these traps.

Betula displays a unique distribution pattern, with similar values in the subalpine zone and in the montane meadows where no local birch trees are currently present (around 20% AP and 500 grains cm^{-2} year^{-1}). In contrast, the alpine sites show significantly higher values (around 35% AP and 1,000 grains cm^{-2} year^{-1}), demonstrating the ability of birch pollen to spread over large distances. However, the high values from the alpine sites suggest another influencing factor. One plausible explanation lies in the phenology of *Betula* flowering combined with specific topographic and snow cover conditions. The summit areas typically have reduced and short-lasting snow cover due to the action of the wind on frozen surfaces, potentially allowing *Betula* pollen from early spring flowering to reach the traps more effectively. In contrast, denser and longer lasting snow cover in the subalpine zone may reduce pollen capture as grains settle on the snow and may be washed away with melting snow. Such wash-off of the pollen of early flowering plants has been noted in comparisons of modified Tauber traps and airborne samplers (Ranta et al. 2008), as well as in higher values of these taxa in moss polsters, which are able to catch pollen from flowing water (Lisitsyna and Hicks 2014). This pattern was not observed for other early flowering wind pollinated trees such as *Corylus* or *Alnus*, possibly due to their much lower regional abundance and lower pollen influx, where it can be outweighed by variations from one year to another.

Fagus pollen is evenly distributed across the zones, suggesting effective vertical transport, consistent with previous studies in other European mountain regions (Tonkov et al. 2001, 2016; Gerasimidis et al. 2006; Cañellas-Boltà et al. 2009; Pidek et al. 2010). Although beech occurs locally near two montane meadow sites, pollen values in these traps only slightly exceed background levels, indicating limited visibility of individual trees in the pollen record, in line with previous findings from mountain regions (Markgraf 1980; Papadopoulou et al. 2022). Therefore, higher pollen values are more likely to represent denser stands of beech, either locally or further away. Pidek et al. (2010) showed that *Fagus* pollen disperses poorly over long distances, as values decline rapidly with increasing distance. However, in the Krkonoše, the strong influence of updraughts must be considered, as they can modify the typical dispersal pattern of pollen and complicate interpretations, but there are no present-day stands of beech for comparison.

Abies pollen values are consistently low across all sites, consistent with its rarity in the region. Although silver fir grows near one trap, its presence is not reflected by pollen values. Slightly higher values recorded in a few traps are probably caused by several exceptional years with very high *Abies* pollen production which were noted by Pidek et al. (2013). However, these peak values of several hundred pollen grains are diluted in the long-term averages of the Krkonoše, resulting in values no higher than 100 grains cm^{-2} year^{-1}.

Corylus occurs only sporadically in the Krkonoše flora, and its pollen values are also low (max 115 grains cm^{-2} year^{-1} and 2.5% AP), illustrating its very low transport potential, though Fontana et al. (2023) noted some long-distance dispersal in the Alps. In contrast, *Quercus*, which does not grow in the study area either (both hazel and oak are restricted to foothills), reaches values exceeding 10% AP above the timberline, demonstrating its high dispersal capacity and effective vertical transport (Tonkov et al. 2001, 2009, 2016; Fontana et al. 2023).

The amount of extra-regional pollen transport is further evidenced by pollen of taxa that are not part of the Krkonoše flora nor of the nearby regional vegetation. Such observations have already been made in the high areas of the Jura mountains, the Pyrenees and the Alps (Markgraf 1980; Cañellas-Boltà et al. 2009; Fontana et al. 2023). In the Krkonoše, taxa such as *Olea* and *Castanea*, which grow more than 200 km away, were occasionally detected. The nearest cultivated *Vitis* (grapevines) are in southwestern Poland and in the České středohoří (central Bohemian uplands). The regular detection of *Ambrosia* pollen is another indication of long-distance transport, coming either from isolated populations in the Czech lowlands or from steppe regions in Slovakia or Ukraine.

Future perspectives

To better understand pollen–vegetation relationships, future research should be extended to forested areas with small openings below the forest limit. Our study was on meadows to enable comparison with the naturally treeless habitats of the arctic-alpine tundra, but limiting our insights into past *Picea*, *Abies* or *Fagus* dominated woods and forests. Integrating direct biomass measurements would help evaluate pollen-biomass correlations, particularly along altitudinal gradients where these relationships appeared to be more complex. These efforts would improve reconstructions of past shifts in the timberline and inform projections of future ecosystem responses. Further methodological comparisons of results from modified Tauber pollen traps with moss polsters could improve interpretations of non-arboreal pollen representation in pollen spectra.

Conclusions

The pollen assemblages from our traps effectively reflected the position of sites relative to the timberline, with a statistically significant distinction between natural treeless arctic-alpine tundra and secondary treeless meadows in the montane zone ($p = 0.001$, PERMANOVA). However, no significant difference was detected between the subalpine and alpine zone, from sites within the treeline ecotone, above the treeline and alpine zone summits. This indicates their broadly similar pollen composition despite substantial differences in the vegetation cover of the mosaic tundra habitats, which receive a high input of long-distance transported pollen, which emerged as the main gradient in the dataset.

The tundra was highly exposed to mountain wind updraughts, which caused a strong input of background pollen, dominated by trees such as *Betula*, *Quercus*, *Alnus* and *Fagus*, together with low but consistent levels from wind pollinated herbs considered as anthropogenic indicators (*Urtica*, *Ambrosia*, *Plantago lanceolata* t., *Artemisia* and Amaranthaceae). Despite the openness of the tundra habitats, these sites showed the highest proportion of arboreal pollen across the altitudinal gradient (~40–60%). In contrast, montane meadows were dominated by local pollen from herbaceous taxa, and the AP values dropped to ~30–50%.

The pollen values of several taxa reflected their abundance in the vegetation quite well. *Calluna vulgaris* was a clear indicator of heaths, Cyperaceae of local peatlands and Poaceae corresponded to their higher local presence in grasslands. *Pinus* values from sites above the forest limit and *Picea* values from below it reflected the local occurrence of pine and spruce by dominating the pollen spectra. Conversely, *Vaccinium*-t. poorly represented its vegetation cover. To sum up, the majority of pollen values of herb taxa represented their local presence either above or below the timberline. However, the vegetation composition of sites above and below it did not produce pollen values distinct enough to allow reasonable differentiation of these habitats by indicator taxa. The pollen assemblages differed more in terms of abundance than in the presence of the various taxa.

Pollen accumulation rates of the sites (PAR-tot) generally correlated with local vegetation biomass, but sites with low biomass had high influxes of long-distance transported pollen. This suggests an inverse pattern: the lower the biomass, the stronger the input of regional pollen. The highest PAR-tot occurred in montane meadows, where high vegetation productivity contributed to high local pollen deposition. In contrast, subalpine bogs and alpine summits recorded the lowest PAR-tot, corresponding to sparse vegetation and increased pollen influx from distant sources.

Pollen threshold values were established for key taxa. *Pinus*, *Betula* and to some extent also *Picea* showed values comparable to those recorded at their boreal limits in Fennoscandia. These values provide valuable references for interpreting palaeoecological records from the Krkonoše and other Central European mountain ranges with comparable environmental conditions.

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Data availability Data are available in the Neotoma Palaeoecology Database, neotomadb.org.

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Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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